Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE
AMERICAN NATURALIST

VOL. XLVI *April, 1912* NO. 544

THE CONTINUOUS ORIGIN OF CERTAIN UNIT CHARACTERS AS OBSERVED BY A PALEONTOLOGIST[1]

DR. HENRY FAIRFIELD OSBORN

RESEARCH PROFESSOR OF ZOOLOGY, COLUMBIA UNIVERSITY, CURATOR EMERITUS
OF VERTEBRATE PALEONTOLOGY IN THE AMERICAN MUSEUM OF
NATURAL HISTORY, VERTEBRATE PALEONTOLOGIST
UNITED STATES GEOLOGICAL SURVEY

ONE method of ascertaining the height of a mountain is with a single instrument, the barometer; another method is by triangulation with several instruments. Thus we may differ from Johannsen in his remark that morphology as a science of great collections in museums is of no value in genetics. The brilliant progress in heredity of the last nine years, beginning in 1903 with the rediscovery of Mendel's law, should not blind us to the four broad inductions from paleontology,[2] that transformation is a matter of thousands or hundreds of thousands of years, that to the living observer all living things may be delusively stationary, that invisible tides of genetic change may be setting in one direction or another observable only over very long periods of time, that discontinuous mutations or saltations may be mere ripples on the surface of these tides.

---

[1] One of the Harvey Lectures of 1912, delivered before the Harvey Society, January 20, 1912. Abstract presented in the Annual Symposium of the Society of American Naturalists, Princeton, December 28, 1911.

[2] Osborn, Henry F., ''Darwin and Palæontology.'' One of the addresses in ''Fifty Years of Darwinism.'' 8vo. Henry Holt & Co., New York, May 1, 1909.

Whatever the truth as to this thought, by a strange paradox it is certain that some stationary characters, some apparently dead things in the eyes of the zoologist and botanist, become movable and alive in the eyes of the paleontologist. Thus a paleontologist comes before the Harvey Society of Physiologists and Physicians with the conviction that his vision is of a different angle from that of the experimentalist, and that by the triangulation of experiment, of anatomy and of paleontology the truth may at least be more nearly approached.

Is there more evidence of discontinuity and of lawlessness, or of continuity and of law, in the origin of new characters? Perhaps no more appropriate question could be chosen as the subject of a lecture in memory of William Harvey, the author of the doctrine of epigenesis, for the essence of this doctrine is that of "successive differentiation of a relatively homogeneous rudiment into the parts and structures which are characteristic of the adult." Paleontology is at one with embryology in the belief that differentiation is in the main gradual and continuous.

Yet to our question the answer prevailing among experimentalists and Mendelians at the present time is that there is little evidence either for continuity or for law; this despite the fact that a large part of the evidence for discontinuity in the origin of characters is most unsound. In fact, our first purpose in this Harvey Lecture is to show how surprisingly unsound this evidence is when we consider that discontinuity has become practically a dogma among a very large number of zoologists and botanists. It is true that the evidence for discontinuity in the *heredity* of characters is as convincing as that for discontinuity in the *genesis* of characters is debatable. Our second purpose in this Harvey Lecture is to show that the evidence for continuity in the genesis of certain characters in man and other mammals is very strong indeed, further, that some of these characters, while apparently continuous in origin, certainly become discontinuous in heredity; from which it follows that discontinuity in heredity constitutes no proof of discontinuity in origin.

The question is, how do these manifold characters of which the body is made up arise, continuously or discontinuously? A conservative opinion from what may be gathered in the whole field of observation at the present time is that while the greater part of evolution is continuous, especially in the origins of certain parts and in the development of certain proportions, there must also be a discontinuity, especially in numerical or meristic structures, such as vertebræ and teeth, and in chemical components and reactions which are essentially antithetic or discontinuous. In other words, there is both continuity and discontinuity, and one problem is to show what is continuous and what is discontinuous.

The history of "characters" is our quest, and now that attention is concentrated all along the line of observation in plants and animals, living and fossil, on the genesis and behavior of single characters, we have laid the train for substantial progress. A vast gain is that which relegates the problem of species to a side issue, or rather to an incidental result of the accumulation of a greater or less number of units.

A "character" may be racial shape of head or length of limb, it may be a cusplet on a grinding tooth, color of hair, or a sportive white lock of hair, it may be the brown or blue color of the eye, it may be the speed of a horse, or the obstinacy of a mule, in short, any structure or function, simple or extremely complex, which is stable and distinct in heredity. A "new character" is something which is unknown before, it may be a new unit, like the horns of cattle, it may be a new form or proportion of such a unit. "I understand by the term unit character," observes Morgan, "any particular structure or function that may appear in heredity independent of other characters. Such unit characters may in themselves be extremely complex and include the possibility of further splitting up.'' The point where Mendelism bears on the problem is, therefore, the continuous or discontinuous origin of the thousands of characters which display this more or less complete discontinuity in heredity.

I. EVIDENCES FOR DISCONTINUITY

Darwin has been widely misunderstood of late as believing in continuity,[3] whereas he chiefly believed in discontinuity.[4] In his original (1859) and final (1872) opinion evolution is due chiefly to the selection of heritable ''individual differences''; these have been understood by some as ''fluctuations.'' His true meaning as to these *individual differences* is to be found in the cases he cited, which may be collected from hundreds of observations in the ''Origin of Species'' and ''Variation of Animals and Plants under Domestication,'' to the effect that such individual differences or *new characters* were in the nature of *minor saltations,* structural or functional, and always hereditary. If we note some of the observations which he assembled in commenting on the genesis of the race horse and the grayhound, breeds which he used by way of illustration of the genesis of new forms in nature, we find they include such suddenly appearing new characters as horn rudiments, taillessness, curliness of the hair, characters which are discontinuous in Bateson's sense, or mutations in that of De Vries;[5] intermingled with these new characters he cited others which are obviously reversional. That he believed in the adding up of minor saltations there can be no question; but on the admirable ground that no evidence had been adduced in nature of evolution by *major saltations,* he rejected St. Hilaire's hypothesis of the natural appearance of entirely new types of animals and plants, or of new or profoundly modified organs; there was no evidence in 1872 and there is none to-day of the sudden appearance in nature of such a breed as the short-legged Ancon sheep. Morgan remarks,[6] ''Darwin undoubtedly supposed that by the continuous selection of minor saltations a character could be slowly shifted in the direction of Selection. This also appears to be the opinion of the conservative mutationists of the present day.''

---

[3] Cf. Poulton, E. B., ''Darwin and the 'Origin,' '' 1909, pp. 49–50. ''His observation and study of Nature led him to the conviction that large variations, although abundant, were rarely selected, but that evolution proceeded gradually and by small steps,—that it was 'continuous' and not 'discontinuous.' '' In answer to this opinion of the most eminent British exponent of pure Darwinism it may be said that *small steps are discontinuities.* (H. F. O.)

[4] Osborn, H. F., ''Darwin's Theory of Evolution by the Selection of Minor Saltations,'' AMER. NATURALIST, Vol. XLVI, No. 542, 1912, pp. 76–82.

[5] In 1909 L. Plate showed clearly that the ''mutations'' of De Vries are practically identical with the ''individual differences'' of Darwin. See ''Darwinismus und Landwirthschaft,'' Berlin, 1909.

Aside from his chief emphasis in the selection of ''individual differences'' Darwin also undoubtedly believed in the selection of *heritable fluctuations of proportion* as illustrated in his classic rebuttal of Lamarck in respect to the long neck of the giraffe:

> So under nature with the nascent giraffe, the individuals which were the highest browsers, and were able during dearths to reach even an inch or two above the others will often have been preserved; for they will have roamed over the whole country in search of food. These slight proportional differences will favor survival and will be transmitted to offspring.

If unusual length of neck in the giraffe, as in man, is a saltatory and heritable character, there is no reason why this classic case also may not strengthen the opinion that Darwin was essentially a mutationist. Fluctuations of proportion, the transmission of which is now in dispute, however, formed a small part of Darwin's scheme, nor was fluctuating variability especially connected by him with the process of evolution.

A very critical reexamination of Darwin's works leads us, therefore, to largely dissent from the influential opinion of De Vries[7] that there was always a doubt in Darwin's mind as to whether "the selection of mutations" or "the selection of extreme variants" played the greater part in the origin of species. As above noted, the actual cases which Darwin cited and his repeated emphasis shows that minor saltations of the De Vries type were chiefly in his mind.

---

[6] Morgan, T. H., letter, January 11, 1912.

[7] De Vries, Hugo, ''Die Mutationstheorie,'' Leipzig, 1901, p. 24.

It is obvious that Darwin could not draw such sharp distinctions either in language or in definition as we may to-day, profiting by forty years of experiment and of analysis.

Let us therefore closely examine the kinds of saltation or discontinuity in mammals which have been recorded during the last fifty years by Darwin, Bateson and others and see what they signify.

1. *Major and Minor Saltations in Mammals as Supposed Material for Selection*[8]

The above exposition of Darwin has a very direct bearing on the problem of continuity and discontinuity because the saltations which he believed to be among the possible materials of natural selection and of evolution were chiefly drawn from the very same sources of evidence, namely, hybridization and artificial conditions of environment, which are now drawn upon by the adherents of discontinuity; the only difference is one of degree, not of kind. The great saltatory characters of Darwin cited below (Table I) in mammals are no more profound than those cited by De Vries as composing the supposed "elementary" species of *Œnothera.* It is therefore interesting to compare twenty distinct types or forms of *major and minor* saltation in eleven different types of mammals. Our authorities are Allen, Azara, Bateson, Brinkerhoff, Castle, Darwin, Davenport, Haecker, Percival, Poulton, Ridgeway, Root, Seton, Sutton, Twining. The accompanying table presents at once the very impressive result obtained by this comparison.

---

[8] The writer is greatly indebted to Dr. Charles B. Davenport, of the Carnegie Institution Station for Experimental Evolution, and to Professor T. H. Morgan, of Columbia University, for criticism and suggestion on this section.

TABLE I

COMPARATIVE TABLE OF SALTATIONS

	1 Man	2 Horses	3 Cattle	4 Sheep	5 Deer	6 Pigs	7 Dogs	8 Cats	9 Rabbits	10 Guinea Pigs	11 Mice
1. Proopic brachycephaly, abbreviation of face. .			×				×				
2. Sudden development of horns on hornless races		×							×		
3. Absence of horns on horned races.			×	×							
4. Supernumerary horns on horned races.				×							
5. Absence of 1 horn on horned races.					×						
6. Jaw appendages.	×			×		×					
7. Taillessness, absence of caudals.	×	×		×				×		×	
8. Earlessness, absence of the external ear.											
9. Single ears, loss of one ear.									×		
10. Short-leggedness, or limb abbreviation			×	×			×				
11. Consolidation of paired hoofs, syndactylism. .			×			×					
12. Polydactylism.	×	×	×	×	×	×	×	×		×	
13. Epidermal thickenings.	×										×
14. Mottled skin markings.	×	×	×			×					
15. Excessive hairiness, or length of hair.	×	×	×	×			×	×	×	×	
16. Hairlessness, entire absence of hair.		×	×				×				×
17. Excessively fine or silky hair.	×		×	×				×	×		×
18. Reversed hairs.			×							×	
19. White hair locks.											
20. Curled-hair.	×	×		×			×				
3*a*. Duplication of horns (transverse).				×							

The very uniformity of the result makes us suspicious as to the significance of saltations, major or minor, in evolution. In eleven different kinds of mammals, namely, man, horses, cattle, sheep, deer, pigs, dogs, cats, rabbits, guinea pigs, mice, we observe that saltations exactly or closely similar repeatedly occur. These saltations are of the same kind, in fact, they partly include those which were regarded by Darwin as possibly part of the evolution process through selection, namely, as stable in inheritance and as under certain circumstances favoring the animals which possessed them.

We evidently have to do with abnormal disturbances of the germinal factors or determiners. Some of these saltations are very stable in heredity and certain of them become widespread; some are prepotent and dominant, others are recessive (*e. g.*, angora, or "long coat" in rabbits, Castle); some (*e. g.*, bent tail in certain mice, Plate) follow neither the Mendelian law nor the principle of blended inheritance.

On the unit-character doctrine we know that one of three things is happening in the germ plasm.

First, a "determiner" may drop out and we see a race of mammals springing up without tails, or color, or hair. In cattle the determiner for horns is dominant, therefore something is added.

Second, a "determiner" may be suddenly lost or modified, and we see excessive hair, curly hair, silky hair, dwarfed or short limbs, brachydactylism.

Third, and even more inexplicable, there occurs the appearance of a new "determiner" or the removal of an "inhibitor" and we observe horns suddenly arising on hornless races like horses and rabbits.

That fancy breeds can be established through the abnormal behavior and selection of these "determiners" there is no question. That nature works through the sudden appearance of new and favorable "determiners" is as yet unproved; it is absolutely disproved in the case of horns, for through paleontology we know that horns arise in a continuous manner. The only mammal known to us at present in which it would appear that a duplicate horn may have sprung into existence through saltation is *Tetraceros,* the four-horned antelope of India. Saltation is possibly of significance in the case of the sudden alteration of hair character because we know of a very considerable number of curly-haired horses in Mexico and South America, which are, however, eliminated by breeders for the reason that correlated with curliness of the hair are apt to arise certain other characters in the hoofs and limbs which are unfavorable.

Under wild or natural conditions in mammals we have as yet secured no direct evidence of such origins or establishment of saltations either major or minor. There is reason to believe that peculiar or anomalous mammals if they do arise are driven away from the herds.

It would appear that the obvious abnormality of the majority of these characters throws the remainder as well as saltatory new characters in general under suspicion of abnormality.

Paleontology, however, furnishes the most direct evidence of the abnormality of saltations in some of the hard parts shown in Table I by presenting counter evidence that such profound changes as abbreviation of the face (proopic brachycephaly), development or loss of horns, reduction or absence of caudal vertebræ, abbreviation or elongation of the limbs, syndactylism or consolidation of separate metapodials have all been established, wherever we know their history, through continuity and not through discontinuity.

2. *Bateson's Evidence (1894) of Discontinuity*

Bateson in 1894[9] was the first to clearly advance the discontinuity hypothesis as a mode of origin of species in its modern form. At the time this work appeared it suffered a searching review from Scott.[10] Mutationists,[11] however, still refer to it as laying the foundations for the discontinuity hypothesis. In order to test the "*Materials for the Study of Variation*" critically in the light of the subsequent advance in paleontology, Dr. W. D. Matthew, who is without bias in the question, was requested to examine all the cases of discontinuity in mammals cited by the author with reference to the question whether or not these cases have any real significance in evolution. He reports:

> Of the 320 cases of discontinuity cited in mammals the greater part are obviously teratological and have no direct significance in relation to paleontologic evolution except for a very few instances such as the supernumerary or fourth molar teeth of *Otocyon*. While not significant [in evolution] these teratological cases are interesting because they show the prevalence of homœosis, and indicate that many of the

---

[9] Bateson, Wm., "Materials for the Study of Variation Treated with Especial Regard to Discontinuity in the Origin of Species," Macmillan & Co., London, 1894.

[10] Scott, W. B., "On Variations and Mutations," *Amer. Jour. Science* (3), Vol. XLVIII, 1894, pp. 355–374.

[11] Darbishire, A. D., "Breeding and the Mendelian Discovery," 8vo, Cassell & Co., London, 1911.

remaining cases which might [otherwise] be considered normal saltations or reversions may actually be teratologic, but disguised by homœosis; all of the possibly significant cases (such as the supernumerary molars) are thereby placed under suspicion. Setting aside this suspicion the minority of the "significant" cases in teeth and feet may be said to afford evidence of the meristic variability of vestigial and rudimentary structures. Bateson's statement that such variability is related not to non-functionalism but to terminal position in a series appears to me directly in conflict with his [Bateson's] own evidence, as it certainly is with all my experience. This accords with commonly observed data in paleontology, for no paleontologist would question that vestigial teeth or bones are apt to [finally] disappear by "discontinuous" evolution. *As to the appearance by saltatory evolution of new and primarily functional parts in teeth or feet, I know of no adequate paleontologic evidence in its favor.* It is either demonstrably false or decidedly improbable. In the cases of supernumerary teeth (*Otocyon myrmecobius,* Cetacea, etc.) saltatory evolution may be regarded as reasonable in default of any paleontologic evidence to the contrary. Meristic or numerical evolution in fully functional vertebræ is intrinsically probable as the only method of evolutionary change.

The fact that so many cases of supernumerary teeth are associated with asymmetry throws doubt on the significance of all such cases; asymmetric variations and those occurring only in upper or only in lower teeth have no analogy in paleontology; such cases as occur abnormally are recognized as of a different and non-significant class than normal evolutionary changes.

A summary of Matthew's report is as follows:

Bateson cites 323 cases of discontinuity in vertebræ, teeth and skull. Of these 286 are abnormal, or teratological, or reversional, and have absolutely no significance in evolution; ten cases of supernumerary (or fourth molar) teeth are possibly significant because among the mammals there are a few genera with fourth molars which may possibly have arisen by saltation. There remain only thirty-seven cases which may be ranked as "probably significant," and these are the meristic additions or reductions of vertebræ in the spinal column, significant because of the well-known variations in the vertebral formulæ of different mammals, and secondly because vertebræ can be added or subtracted only discontinuously.

SUMMARY OF BATESON'S 323 CASES

	Non-Significant	Possible Significant	Variations Vestigial or Reversional
I. Vertebræ	17 (asymmetry)	27*	
II. Teeth	83	10†	67
III. Feet	110		
	210	37	67

* Numerical variations of cervical, dorsal and lumbar vertebræ.

† Additional molars, cf. *Octocyon, Myrmecobius, Cetacea.* Six cases insufficiently described.

The fact that the vast majority of germinal anomalies examined in the above review of Darwin and of Bateson have no significance in evolution in a state of nature, throws all germinal anomalies under suspicion as natural processes, important as they may be in artificial breeding and hybridizing. Yet some of these anomalies in mammals are less profoundly discontinuous than those which De Vries has cited in plants under the designation of ''mutations.'' The most important of these De Vries' mutations may now be considered.

3. *Evidence for De Vries's Mutation Theory*

In 1901 the biological world was aroused as it had not been since 1859 by the publication of De Vries's hypothesis.[12] Here was a new and apparently sure foundation for discontinuity in the supposed sudden appearance of *elementary species* or ''mutants'' arising with the acquisition of entirely new characters, new forms of plants or animals quite free from their ancestors and not linked to them by intermediates. The influence and vitality of this great work is shown in a citation from Darbishire (1911, *op. cit.*, p. 5):

> The view that species have originated by mutation is based on Prof. de Vries' observations on the Evening Primrose (*Œnothera Lamarckiana*) (Fig. 1). Working with this form, he was able to witness, for the first time, the actual process of the origin of new species.

[12] De Vries, Hugo, ''Die Mutationstheorie,'' Leipzig, 1901, p. 24.

Critical analysis during the past two years by Davis and by Gates[13] of the very species *Œnothera Lamarckiana* on which De Vries chiefly based his monumental work, tends to show that *O. Lamarckiana* is possibly a hybrid of *O. biennis* and *O. grandiflora* and not a natural species. Thus the "elementary species" which are springing from it in various gardens may prove to be comparable to the familiar results of hybridization in mammals and birds.

Davis, on the basis of his prolonged experimental researches, says:

> Indeed, the theory of De Vries may fairly be said to rest chiefly upon the behavior of this interesting plant, the account of which forms so large a part of his work "Die Mutationstheorie" (2 vols., Leipzig, (1901). . . . In a brief perusal of the work one is struck by the optimism of its author and the brilliancy and breadth of his exposition of the views set forth. . . . The analysis of the data amassed by Darwin, in which it is shown that Darwin's "single variations" are the same as De Vries's mutations seems to the reviewer particularly effective. . . . Probably the time will soon come when nearly all biologists will be ready to admit that mutation or the sudden appearance of new forms has been an important factor at least in species formation of plants and animals. Admitting this it remains to be discovered what relation these sudden appearances bear to *the general trends of evolution which are apparent in so many phylogenies* [italics our own] . . . for granting the facts of mutation we have only accounted for a micro-evolution, and it is still to be shown that the larger tendencies can be sufficiently accounted for by the same means without the intervention of other factors. . . .

The skepticism of both these botanists is striking. Their opinions as to the existence of larger evolutionary trends are exactly in accord with those of paleontologists.

4. *Evidence for Discontinuity from Mendelian Heredity and Experimental Selection*

The newest bulwark of the discontinuity hypothesis is that erected since 1903 by the revival of the great discovery of Mendel (1865) and by the negative results of experiments on fluctuating or quantitative variation.

---

[13] Davis, Bradley Moore, "Genetical Studies on Œnothera. II. Some Hybrids of *Œnothera biennis* and *O. grandiflora* that resemble *O. Lamarckiana*," AMER. NATURALIST, Vol. XLV, April, 1911, pp. 193–233. Gates, R. R., "Mutation in Œnothera," AMER. NATURALIST, Vol. XLV, No. 538, October, 1911, pp. 577–606.

From the prevalence of discontinuity in heredity, the separateness of ''unit characters'' as they appear in the body and the equally sharp separableness of their complex of ''factors,'' ''determiners'' or ''genes'' in the germ has arisen the theoretical assumption of *the discontinuity of origin of all characters in the germ.* We shall now show that this assumption is a *non-sequitur.*

First, however, the truly marvelous and epoch-making Mendelian discoveries require our especial examination in their bearing on the problem of continuity and discontinuity. We have reviewed[14] the contributions of Allen, Bateson, Castle, Cannon, Cuénot, Darbishire, Davenport, Durham, Farrabee, v. Guita, Haacke, Hagedoorn, Harmon, Hurst, Laughlin, Morgan, Pearson, Plate, Punnett, and Rosenoff. This review covers unit characters only as observed in mammals, to which none the less the principles discovered by Mendel in the common garden pea (*Pisum sativum*) apply with striking uniformity.

The prevailing field of the researches of these talented investigators in mammals has been in color characters, chemical in essence, in various species of rodents, chiefly mice and guinea pigs, also in Ungulates, such as horses and cattle, the latter studied less by experiment than from stud books. Hair form in rodents and in man and skin pigment have also been exactly investigated. The most striking general result is the principle of antithesis of characters which mutually exclude each other, as typified by the antithesis of Mendel's ''tallness'' and ''shortness'' in peas.

The second great feature is that when these antithetic characters meet in the germ cells, one dominates over the other; this dominance is a sort of perpetual prepotency. ''Prepotency,'' observes Darbishire, ''is an attribute of individuals and capricious in its appearance. . . . Whatever be the nature of this power . . . it is clear that it has nothing to do with dominance . . . dominance is an invariable attribute of particular characteristics."[15] Plate (1910), on the contrary, observes, "But a variety of facts seem to indicate that a reversal of dominance may occur under certain circumstances and a dominant character may become recessive, and *vice versa*."[16] Such reversal of dominance would appear to be the case in a comparison of the mule (cross between ass ♂ and horse ♀) and the hinny (cross between the horse ♂ and the ass ♀).

---

[14] With the aid of Miss Mary M. Sturgess, now attached to the Carnegie Institution Station for Experimental Evolution at Cold Spring Harbor, L. I.

When antithetic characters or functions meet in heredity, there is either "prepotency," or "dominance," or "recession" (*i. e.*, latency), or "inhibition," a something which indirectly prevents the appearance of characters, or "imperfect dominance," or "blending." In brief, there are *degrees* of separableness and antithesis.

Dominance, Conservative or Progressive.—It will be seen at once that progressive evolution through discontinuity would depend on the *dominance of racially new characters and types*. The experimental evidence is conflicting, it does not show that new characters are necessarily dominant.

There are many instances of dominance of wild species (older type) over domesticated species (newer type); thus De Vries suggested (1902) that the dominant characters are those which are racially older. One case among the mammals is that the wild gray color in mice dominates over grades below it, black, brown, and white (Plate, 1910).

Examples of dominance in single characters are that more intense dominate over less intense colors (Plate, 1910, Davenport, 1907); in the eyes, brown over gray, gray over blue; in the skin, brunettes over blondes (Davenport, 1909), piebalds over pure albinos (Plate, 1910). In the hair, wavy or spiral forms dominate over straight (Davenport, 1908). This would have some bearing on the discontinuous fading out of color in desert races like the quagga, which lost all the stripes of its relative the zebra.

---

[15] Darbishire, *op. cit.*, p. 96.

[16] Plate.

The idea that the positive or present character dominates over the negative, latent or absent character has become the prevailing one.

> It seems highly probable, observes Davenport (1910), that the future will show that many more advanced or progressive conditions are really due to one or more unit-characters not present in the less advanced condition. In that case it will appear that there is a perfect accord in the two statements that the progressive and the "present" factor are dominant (pp. 89–90) . . . the specific characteristics are mostly those that appear late in ontogeny (p. 86) . . . the potency of a character may be defined as the capacity of its germinal determiner to complete its entire ontogeny. If we think of every character as being represented in the germ by a determiner, *then we must recognize the fact that this determiner may sometimes develop fully, sometimes imperfectly and sometimes not at all* [italics our own]. . . . When such a failure occurs in such a normal strain a sport results. . . . Potency is variable. Even in a pure strain a determiner does not always develop fully and this is an important cause of individual variability (Davenport, 1910, p. 92).

Plate similarly favors the hypothesis of dominance of newer or progressive characters. He observes (1910):

> The [Mendelian] laws of inheritance favor progressive evolution in two ways, for . . . higher, more complicated characters are generally dominant to the lower, and . . . qualitative characters usually follow the Mendelian principle in the case of closely related forms (races, varieties) while in the crossing of species they follow intermediate [or blended] inheritance as a rule. In the latter case there is the possibility that the crossing may have a swamping effect, but this can play no large rôle on account of the infrequency of hybrids between species (Plate, 1910, p. 606).

The same author is of the opinion that phyletic evolution is discontinuous as regards the transformations of the determinants [determiners], but in most cases is continuous in their visible outward workings. He thus maintains that while germinal transformations are discontinuous there may be no real antithesis between continuous and discontinuous somatic variation.

Thus Mendelians appear to agree, *first,* that there are *grades of continuity and discontinuity,* that there are antithetic characters which are sharply discontinuous, others which are partly continuous, blended or intermediate. *Second,* it would appear that complete discontinuity or entire dominance or recession are qualities in heredity *which may gradually evolve.* Many characters show imperfect dominance (Castle, 1905); gametic purity is not absolute (Castle, 1906); selection is of importance in the improvement of races (Castle, 1907). There are a number of truly blending characters, such as lop-earedness in rabbits (Castle, 1909), cross blends of long and short hairs (Castle, 1906), cross blends between short- and lop-eared rabbits which are permanent (Castle, 1909), blends in weight inheritance and in skeletal proportion (Castle, 1909).

More recent work has tended to show (Hatai, 1911)[17] that blended inheritance may be considered to be a limited case of alternative inheritance where dominance is imperfect. Thus Mendel's law of alternative inheritance may be considered as the standard in all the cases referred to it (Hatai, 1911, p. 106). Certain characters which were considered formerly to blend are now regarded as showing a certain kind of segregation or unit inheritance. Thus Davenport (1909) observes:

> Skin pigment does not show thorough blending inheritance, but segregation (sometimes imperfect), a more pigmented being imperfectly dominant over a less.[18] . . . The reason, the same author observes (1909, for the blending of hair and skin color in man is the non-development of distinct color unit-determiners owing to the fact that in man for a long period there has been no selection for intensity of color, whereas in the lower mammals definite color determiners have long been maintained by selection.

Thus the prevalent recent opinion among Mendelian observers is *that there is a real discontinuity between the germinal or blastic characters and what the paleontologist or morphologist generally observes, is only an apparent continuity between somatic characters.*

---

[17] Hatai, Shinkishi, "The Mendelian Ratio and Blended Inheritance," AMER. NATURALIST, Vol. XLV, No. 530, February, 1911, pp. 99–106.

[18] Pigmentation of the skin seems to depend in man on a series of color intensity units, possibly one or a few large units, more probably a number of small units so close together as to be almost continuous (Davenport, 1910).

Since, however, the behavior of somatic characters forms our only means of knowing whether the determiners are continuous or discontinuous, it is obvious that this opinion requires further examination in the conceptions of Johannsen.

5. *Johannsen's Pure Line Theory*[19]

The theoretic contrast between the real discontinuity of the blastic determiners and the delusive continuity of visible or somatic form is pushed to its extreme in the "pure-line" conception which marks the latest development in heredity, an advance upon Weismann's germ-plasm theory and Mendel's unit-character law. Through experiments on successive generations of self-fertilizing plants (the garden bean), Johannsen has reached a standpoint which may be briefly stated as follows:

> A "pure line" is composed of the descendants of one pure strain or homozygotic organism exclusively propagated by self fertilization; such pure lines demonstrate the stability of hereditary constitution in successive generations where undisturbed by cross breeding or mingling with other strains, showing that the only real changes in organisms are those due to the sudden appearance of new determiners in the germ.
>
> To replace the word *determiner* the term *gene* is proposed. The *genotype* represents the sum total of all the genes in the fertilized germ cell, gamete or zygote; we do not know a genotype but we are able in experiment to demonstrate "genotypical differences." The *biotype* is a group of similar genotypes or pure strain individuals.
>
> Gene, genotype, and biotype are not seen; they are the smaller and larger units of heredity.
>
> The phenotype is what we see; it is the developing organism. Morphology supported by the huge collections of the museums has operated with "phenotypes" in phylogenetic speculation. It is thus a science of phenotypes and is not of value in genetics because phenotype description is inadequate as the starting point for genetic inquiries. The adaptation of phenotypes through the direct influence of environment [Buffon's factor] or of use and disuse [Lamarck's factor] is not of genetic importance. Ontogenesis is a function of the

---

[19] Johannsen, W., "The Genotype Conception of Heredity," AMER. NATURALIST, Vol. XLV, No. 531, March, 1911, pp. 129–159.

genotype, but the genotype is not a function of ontogenesis. The idea of evolution by continuous transitions from one type to another has imposed itself upon zoologists and botanists, who are examining chiefly shifting phenotypes in very fine gradations. There is such a continuity in phenotypes but not in the genotypes from which they spring. All degrees of continuity between phenotypes may be found, but real genetic transitions must be distinguished from the transitions which we find in museums.

Genotypes, it is true, can only be examined by the qualities and reactions of the phenotypes.

Such examination shows that within pure lines—if no new mutations or other disturbances have been at work—there are no genotypical differences in the characters under examination. The only real discontinuity is that between different genotypes. The mutations observed in nature have shown themselves as considerable discontinuous saltations. There is no evidence for the view that mutations are practically identical with continuous evolution. In pure lines no influence of special ancestry can be traced; all series of progeny keep the genotype unchanged through long generations. Discontinuity between genotypes and constant differences between the genes show a beautiful harmony between Mendelism and pure line work.

Selection will have no hereditary influence in changing genotypes. Even the selection of fluctuations in pure lines is ineffective to produce a new genotype.

Heredity may thus be defined as the presence of identical genes in ancestors and descendants, or heredity stands for those properties of the germ cells that find expression in the developing and developed phenotype.

Similarly Jennings observes:[20] What distinguishes the different genotypes, then, is *a different method of responding to the environment.* And this is a type of what heredity is; *an organism's heredity is its method of responding to the environmental conditions* [p. 84]. . . . It appeared clear, and still appears clear, that a very large share of the apparent progressive action of Selection has really consisted in the sorting over of preexisting types, so that it has by no means the theoretical significance that had been given to it [p. 88]. . . . I had hoped to accomplish this myself, but after strenuous, long-continued and hopeful efforts, I have not yet succeeded in seeing Selection effective in producing a new genotype. This failure to discover Selection resulting in progress came to me as a painful surprise, for like Pearson I find it impossible to construct for myself a "philosophical scheme of evolution," without the results of Selection and I would like to see what I believe must occur [pp. 88–89]. . . . It would seem that the diverse genotypes must have arisen from one, in some way, and when we find out how this happens, then such Selection between genotypes

> will be all the Selection that we require for our evolutionary progress [p. 89].

Thus Johannsen's general conception of the origin of progressive or retrogressive new characters is that "it is sufficient to state that the essential point in evolution is the alteration, loss or gain of the genes or constituents of the genotype . . . all evidences as to 'mutations' point *to the discontinuity of the changes in question.*"

6. *Negative Results of Experiments on Quantitative Variation*

We agree with Johannsen that a delusive *appearance* of continuity might arise through selection of degrees of hereditary fluctuation in structure or function, for example, of tallness or shortness of stature, of intensity or faintness of color. Some Mendelians discard fluctuations altogether as non-hereditary; thus Punnett (1911, p. 138)[20] observes: "At the present time we have no valid reason for supposing that they [fluctuations] are ever inherited."

The question, however, is not as to quantitative ontogenic variations caused by favorable or unfavorable environment or by changes of habit, but as to heritable fluctuations springing from the germ plasm. Experiments have been directed to the point whether variations in size, in proportion, etc., of unit characters as distinguished from the unit characters themselves are transmitted.

Davenport has reached negative results; he observes (1910):

> In the last few decades the view has been widespread that characters can be built up from perhaps nothing at all by *selecting in each generation the merely quantitative variation that goes farthest in the desired direction.* The conclusion upon which De Vries laid the greatest stress, that quantitative and qualitative characters differ fundamentally in their heritability, is supported by our experiments (p. 96). I have made two tests of this view using the plumage color of poultry

---

[20] Punnett, R. C., "Mendelism," Macmillan Co., 1911 (3d edition).

(p. 94). . . . After three years of selection of the reddest offspring no appreciable increase of the red was observed except in one case, which looks like a sport (p. 96). These fluctuating quantitative conditions depend on variations in the point at which the ontogeny of the character is stopped; and the *stopping point* is in turn often if not usually determined by external conditions which favor or restrict the ontogeny. Thus the selection of redness of comb, of polydactylism, of syndactylism, have not proved the inheritance of quantitative variations. Apparently, within limits, these quantitative variations have so exclusively an ontogenic signification that they are not reproduced so long, at least, as environmental conditions are not allowed to vary widely.

Similarly Love[21] from experiments on the yielding power of plants remarks:

> Unless further studies produce different results we can say from the facts at hand that there is no evidence to show that a basis exists for cumulative selection.

Similar conclusions have been reached by Pearl (1909)[22] in the breeding of fowls for laying purposes.

All the above results are negative.

Even the positive or affirmative results obtained by Cuénot and later by Castle, wherein quantitative characters may be shifted in one direction or the other by selection are now given a new interpretation by certain Mendelians. For example, Cuénot showed by continued selection of lighter colored mice that the coat became paler; and Castle has shown that in rats the coat through selection may be made darker. Castle remarks (1911):[23]

> I prefer to think with Darwin that selection . . . can heap up quantitative variations until they reach a sum total otherwise unattainable, and that it thus becomes creative.

He cites cumulative results in the development of a fourth toe in the hind foot of guinea-pigs and in the modification of the dorsal striping of hooded rats.

---

[21] Love, Harry H., "Are Fluctuations Inherited?" Contr. VI, Lab. Experim. Plant-Breeding, Cornell Univ., AMER. NATURALIST, Vol. XLIV, No. 523, July, 1910, pp. 412–423.

[22] Pearl, Raymond, "Is there a Cumulative Effect of Selection?" Abstammungs- und Vererbungslehre, 2, 1909, H. 4.

[23] Castle, W. E., "The Nature of Unit Characters," The Harvey Lectures, delivered under the Auspices of the Harvey Society of New York, 8vo, J. B. Lippincott Co., pp. 90–101.

Morgan's remarks (1912) on these positive experiments are as follows:

> Castle has been very guarded in regard to the *interpretation* of the results of selection in this case. It is probable that extreme selection is necessary to maintain the higher stage reached. It does not breed true and slips back easily. If this is correct it suggests: first, that nothing permanent has been effected in the germ-cells; and second, that the result is due to the discovery of more extreme cases of fluctuating variations than ordinarily occur.

The general import of these experiments and opinions is that fluctuations in the determiners, or genes, can not be utilized to establish a new quantitative mean. It is obvious that what have been measured by biometricians as hereditary "fluctuations" might be regarded as "saltations" of all degrees, but such saltations do not represent *new* determiners in the Mendelian or Johannsen sense; they are mere fluctuations in existing determiners. Pure Mendelians would allege that tallness in man or other mammals can only be accumulated through the saltatory origin of "tall" determiners which are not connected continuously through intermediate forms with the antithetic "short" determiners. As to stature Brownlee observes (1911, p. 255):[24]

> I think that I have shown that there is nothing necessarily antagonistic between the evidence advanced by the biometricians and the Mendelian theory. . . . (1) If the inheritance of stature depends upon a Mendelian mechanism, then the distribution of the population as regards height will be that which is actually found, namely, a distribution closely represented by the normal curve.

6. *Summary as to Discontinuity and Mendelism*

Genetics is the most positive, permanent and triumphant branch of modern biology. Its contributions to heredity are epoch-making. But heredity is the conservative aspect of biology, and experimental genetics thus far reveals the laws of conservation.

---

[24] Brownlee, J., "The Inheritance of Complex Growth Forms, such as Stature, on Mendel's Theory," *Proc. Roy. Soc. Edinburgh,* Vol. XXXI, Pt. II, 1911, pp. 251–256.

Genetics has not yet brought us one single step nearer the solution of the problem of the progressive origin of new characters in mammals. The very independence, multiplicity and discontinuity of the units leave us farther afield. In place of what used to be regarded as the instability of the organisms, as a whole, we now have to conceive of the instability of thousands, nay hundreds of thousands of units.

As shown in our analysis of the saltations cited by Darwin and Bateson, Mendelism has revealed the fact that the majority of saltations simply reflect failures in the germinal mechanism. The inference is natural that the remaining minority also represent anomalies, or lawless conditions. Over a half century of anatomical research among mammals has failed to demonstrate in a state of nature the sudden origin of a single new progressive character which has become fixed in the race.

Nor have Mendelism and experimentalism released us from the hard confines of examination of the germ through the soma; behavior of unit characters in the soma is the sole means of knowing the behavior of the "determiners" in the germ. If the unit characters in the soma behave discontinuously we are forced to the conclusion that their determiners behave discontinuously; if, on the contrary, these unit characters behave continuously, are we not forced to the conclusion that there is a continuity in the behavior of the corresponding determiners?

Let us therefore proceed to consider the value of some of the evidence for continuous behavior in the origin of certain new characters, again repeating our opinion that certain other characters are antithetic, without intermediates, and consequently discontinuous both in heredity and in origin.

(*To be concluded*)